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PRE- AND POSTPRANDIAL MOSQUITO RESTING BEHAVIOR AROUND CATTLE HOSTS

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ABSTRACT. Spatial distribution of mosquitoes around a bovine host was studied in November 1997 in northern Thailand (17°38′N, 99°23′E). Forty bamboo stakes were arranged 1 m apart, in 4 rays of 10, around a cow tethered in an open field. All mosquitoes found resting on the stakes were collected by aspiration between 7:00 p.m. and 11:00 p.m., sexed, and identified to species; and feeding status was categorized as fed or unfed. Collections were repeated over 8 nights, with and without the host cow. A total of 1,566 mosquitoes from 25 species (5 genera) was collected. *Anopheles aconitus* was the most abundant species (643 individuals), followed by *An. peditaeniatus, Culex vishnui,* and *Cx. pseudovishnui.* We found that the number of mosquitoes collected from the stakes was related to the presence of the cow host; the number of mosquitoes collected was unrelated to the compass point location of the bamboo stakes, with the exception of *Mansonia uniformis*; unfed mosquitoes preferred bamboo-stake resting sites that were closer to the host; the daily fed to unfed ratio of the dominant species was negatively correlated with the daily total number of mosquitoes collected; and fed and unfed mosquitoes clustered in interspecific heterogeneous groups around the host cow. Cluster analysis separated the species into 2 groups. The 1st consisted of 5 species with higher proportions of fed mosquitoes, whereas the 2nd, represented by 7 species, aggregated around the host within a distance of 1–4 m with lower proportions of fed mosquitoes. The interspecific variation in the distribution of unfed females was presumed to be due to a lack of feeding success. We discuss the significance of prebiting resting. In cases in which large numbers of mosquitoes are present, prebiting resting can be adaptive to avoid host defensive behavior triggered by attacking mosquitoes.

KEY WORDS Mosquito, bloodfeeding behavior, resting, *Anopheles aconitus, Culex vishnui* species group

INTRODUCTION

The bloodfeeding behavior of mosquitoes is an important aspect of the epidemiology of mosquitoborne diseases. Mosquito bloodfeeding behavior consists of several phases: the search for potential hosts, attraction to hosts, attacking, feeding, and resting. Of these phases, much attention has focused on preattack behavior because of its practical importance. The interval between the appearance of a mosquito and when it alights on the host is called the prebiting rest (Reid 1968) or preattack resting (Clements 1999). A prebiting rest has been reported in several taxa (Service 1993), including the *Anopheles leucosphyrus* group (Colless 1956a, 1956b), *An. dirus* Peyton and Harrison (Scanlon and Sandhinand 1965), *An. gambiae* s.l. (Smith 1958), *Culex quinquefasciatus* Say (De Meillon and Sebastian 1967), *Cx. tritaeniorhynchus* Giles (Wada 1969), and *Mansonia* spp. (Wharton 1962, Service 1969). Females subsequently rest while digesting the blood meal, presumably because the added weight makes flight both difficult and dangerous. Field observations suggest that many mosquito species approach the host and remain nearby for some time before attacking. The biological significance of this prebiting rest is unknown and preattack distribution has been poorly studied. Understanding the spatial distribution of mosquitoes around hosts can provide practical information for vector control. This preattack period possibly provides an opportunity for the mosquito to distinguish among host species and become stimulated to bite. In this study, we examined the spatial distribution of mosquito species around the host before and after feeding.

MATERIALS AND METHODS

Study site: Studies were conducted in the countryside near Ban Den Udom, Amphoe Thoen, Changwat Lampang, northern Thailand (17°38′N, 99°23′E) on November 10–17, 1997. Ban Den Udom is located in a wide valley (Huai Mae Mok) covered by paddy fields, which were dry at the time of the study. A 25-m² grassy plot (approximate height of the grass, 50 cm) was chosen as the study site. Neither human dwellings nor animal sheds were located near the site. The nearest human residence, a temple, was several hundred meters away.

Methods: We modified the sampling method used by Wada (1969). Figure 1 illustrates the study design. After clearing the grass, 40 bamboo stakes (0.7 m high × 4 cm wide) were pushed into the ground to serve as resting substrates. They were located at the 4 points of the compass in rays of 10 stakes, with 1-m spacing between stakes. From 6:00 p.m. until the following morning, 1 cow was tethered in the center of the plot. Mosquitoes resting on the sides of the stakes were collected by 2 people by using aspirators for 20 min at 7:00, 8:00, 9:00, 10:00, and 11:00 p.m. The collected specimens were kept alive in separate bottles, which were sorted by compass point and distance from the host cow. The following morning, the mosquitoes were

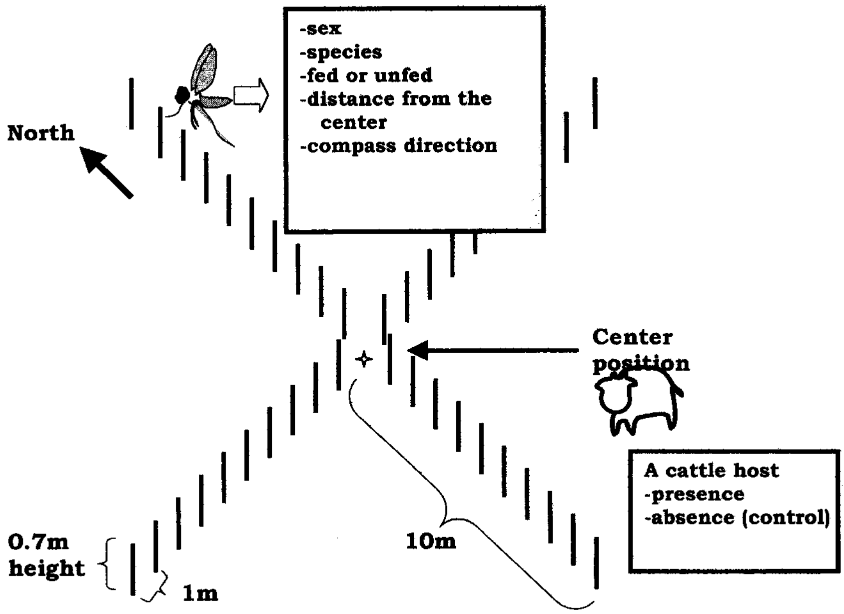

Fig. 1. Illustration of the study design. The parameters recorded are the number, sex, engorgement state, and species of moquitoes resting at the 40 stakes along arrays, in the presence or absence of a cattle host.

identified by sex, species, and state of engorgement (categorized as fed or unfed). Collections were made on 8 nights. A control set without the host cow was replicated over 2 nights, on November 13 and 14, to differentiate those mosquitoes that were attracted to mosquito collectors, if any.

Table 1. Species composition of mosquitoes captured at bamboo stakes during November 10–17, 1997.

Species	Females	Males	Total
Anopheles aconitus	638	5	643
An. peditaeniatus	173		173
An. nivipes	98		98
Ar. subalbatus	38		38
An. minimus	33		33
An. splendidus	12		12
An. barbirostris	10		10
An. kochi	7		7
An. tesselatus	7		7
An. sawadwongporni	3		3
An. willmori	3		3
An. annularis	1		1
Culex pseudovishnui	152		152
Cx. vishnui	133		133
Cx. tritaeniorhynchus	57	1	58
Cx. gelidus	37	1	38
Cx. whitmorei	18		18
Cx. fuscocephala	15		15
Cx. bitaeniorhynchus	1	1	2
Cx. quinquefasciatus	1		1
Aedes vexans	51		51
Ae. lineatopennis	21		21
Ae. albopictus	2		2
Mansonia uniformis	26	20	46
Ma. crassipes	1		1
Total	1,538	28	1,566

Spatial distribution: Canonical correspondence analysis (CCA) was used to determine how mosquito abundance on the stakes relates to presence or absence of the host cow among the 4 compass directions and distance (Program CANOCO ver. 4.0, Center for Biometry, Wageningen, Netherlands). To increase statistical reliability, only species that were represented by more than 20 females were included in the analysis. The number of mosquitoes was not transformed, and the number of permutations was 199.

Correlation of proportion fed and mosquito abundance: By using regression analysis, we also determined the effect of mosquito abundance on the ratio of the fed mosquitoes. We defined mosquito abundance as daily total catch of all mosquito species, whereas proportion fed was calculated as daily value of each species. For statistical strength, only species with samples of at least 50 females were included in the analysis.

Patterns of mosquito distribution around the host: To clarify the general pattern of mosquito attack behavior, we clustered the species according to the ratio of fed mosquitoes to the total collected in each distance category. Because of low sample sizes at some stakes, data from the stakes were combined into 3 categories: 1, 2–4, and 5–10 m from the tethered cow. Again, only those species for which more than 20 females were sampled were analyzed. The value $p_{f,d} = n_{f,d}/N$ was calculated for each species, where $n_{f,d}$ is the number of fed or

Table 2. Number of female mosquitoes captured and fed ratio during the study period of November 10–17 1997.

	Host (cow) present						Host (cow) absent	
	Nov. 10	Nov. 11	Nov. 12	Nov. 15	Nov. 16	Nov. 17	Nov. 13	Nov. 14
Fed ratio[1]	0.241	0.200	0.198	0.335	0.303	0.440	0.000	0.000
No. fed females	84	65	67	56	81	33	0	0
No. females	348	325	338	167	267	75	8	10

[1] Fed ratio is defined as number of fed mosquitoes divided by total number of female mosquitoes collected.

unfed females collected at distance *d,* measured from the center of the plot (i.e., where the cow was tethered), and *N* is the total number of female mosquitoes of that species collected. The resulting data matrix represented each mosquito species as a row of $p_{f,d}$ values for each distance category (the columns), and different clustering analyses were applied to the matrix of multispecies $p_{f,d}$. We used 7 clustering strategies (weighted and unweighted average, complete, Ward minimum variance, single, centroid, and median) to examine the Euclidean distance matrix. The distributions of obvious clusters around the host were compared. Bonferroni corrected *t*-tests were used to compare the average distribution of groups in the 3 distance categories. The ratios of fed to total females also were tested for significance with the *t*-test. Proportional data were arcsine-transformed before parametric analyses were applied. These statistical analyses were performed with STATISTICA Professional (1998 Edition, StatSoft Co., Tulsa, OK).

RESULTS

Species abundance and sex ratio

A total of 1,566 mosquitoes belonging to 25 species in 5 genera was sampled (Table 1). *Anopheles aconitus* Dönitz was the most common (643 individuals), followed by *Anopheles peditaeniatus* (Leicester), *Culex pseudovishnui* Coless, and *Cx. vishnui* Theobald (Table 1). Most of the mosquitoes were females (98.2%). Twenty of the 28 males collected were *Mansonia uniformis* (Theobald), and only this species had an even sex ratio (female : male = 1.3; Table 1).

Spatial distribution

The CCA showed that the distribution of mosquito species among the 40 stakes was significantly affected by the presence of a cow, followed by the distance from the cow and orientation of west to east but not north to south (P = 0.010, 0.005, 0.005, and 0.135, F-ratio = 4.20, 3.87, 2.71, and 1.56, respectively).

An average of 253 (range 75–348) mosquitoes was collected daily on the bamboo stakes surrounding the tethered cow, whereas only 8 females were collected on November 13 and 10 female mosquitoes were collected on November 14 without a host (Table 2). Although it was impossible to eliminate the effect of collectors on the species and numbers of resting mosquitoes, the results showed that most of the collected mosquitoes were attracted to the cattle host. The presence of the cow explained 52.5% of cumulative percentage variance of the species–environment relationship, whereas the 2nd east–west factor (if the number of mosquitoes collected differed north vs. south and west vs. east) was 75.7% and the 3rd distance factor (if the number of mosquitoes collected was related to the distance from the center) was 93.8%.

A significant difference was noted among the numbers of mosquito species collected at the compass points of west to east but not north to south. This was because of *Ma. uniformis,* more of which were collected in the east row. Because the other species did not show such a tendency, they were presumed to be randomly distributed before approaching the host.

We found significant correlations between the number of resting female mosquitoes and the dis-

Table 3. Spatial distribution of the number of mosquitoes resting at the stakes at 1–10 m from the center with and without a cattle host.

Mosquito sex	Engorgement	Host	Total catch	Distance from the center (m)									
				1	2	3	4	5	6	7	8	9	10
Female	Fed	Present	386	175	93	57	24	18	3	6	3	6	1
	Fed	Absent	0	0	0	0	0	0	0	0	0	0	0
	Unfed	Present	1,134	466	335	171	75	40	20	12	9	3	3
	Unfed	Absent	18	6	4	1	0	1	1	1	1	2	1
Male		Present	22	6	1	6	2	2	1	1	2	1	0
		Absent	6	0	0	0	2	1	0	2	1	0	0

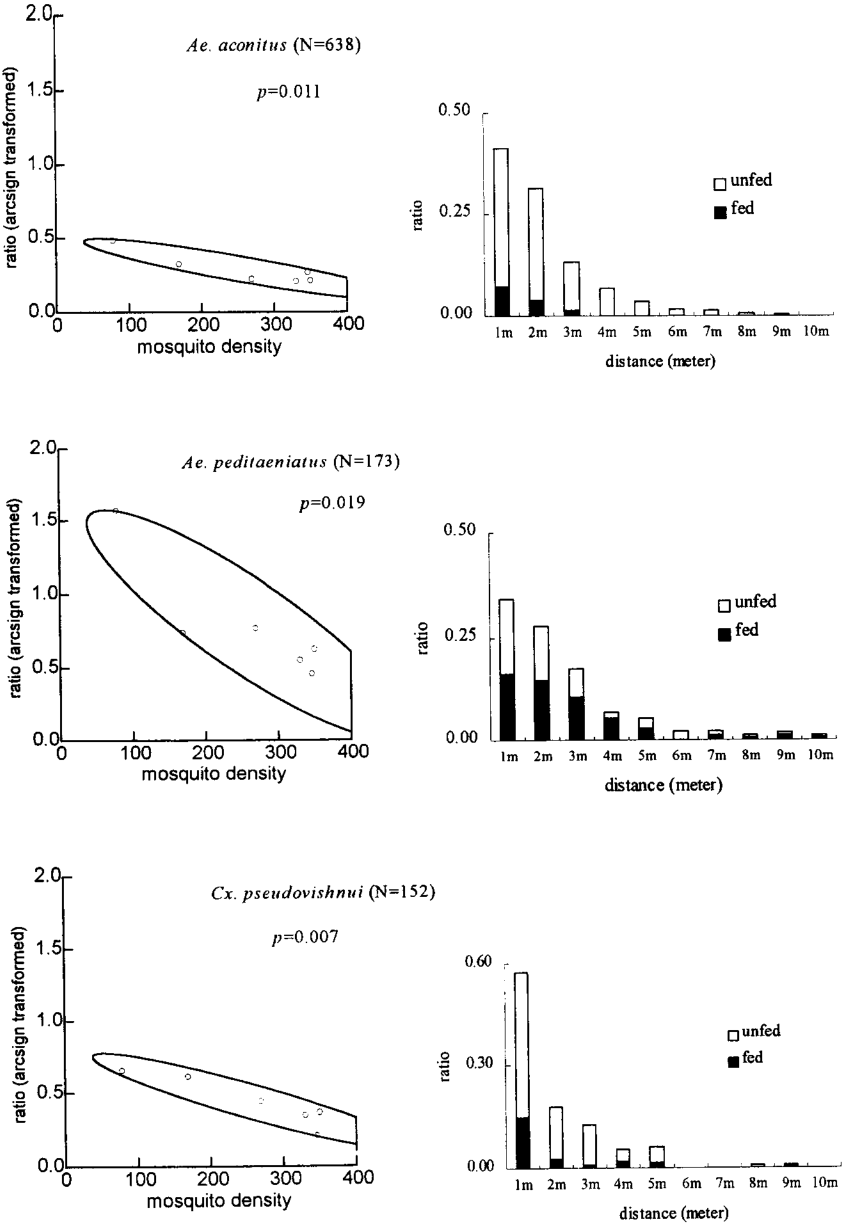

Fig. 2. Regressions with probability values (analysis of variance) of 7 dominant culicine species among daily fed ratio of each species (vertical axis) and daily total catch of all species (horizontal axis) with their spatial distribution from the host.

tance from the host. The distribution of mosquitoes around the host is shown in Table 3 and Fig. 2. It shows both fed and unfed resting mosquitoes concentrated within 5 m from the host.

Correlation of proportion that had fed and number of resting mosquitoes

Seven species were represented by more than 50 females (Table 1). Regressions of the daily number of resting mosquitoes collected vs. the daily ratio of fed to total number are shown in Fig. 2. In 4 of the 7 species (*An. aconitus, An. peditaeniatus, Cx. pseudovishnui,* and *Cx. vishnui*), the regression was significantly negative (analysis of variance [ANOVA], $P = 0.011$, 0.019, 0.007, and 0.021, respectively). No significant correlation was found for the other 3 species (*Anopheles nivipes* (Theobald), *Culex tritaeniorhynchus* Giles, and *Aedes vexans* (Meigen)) (ANOVA, $P = 0.074$, 0.148, and 0.123, respectively).

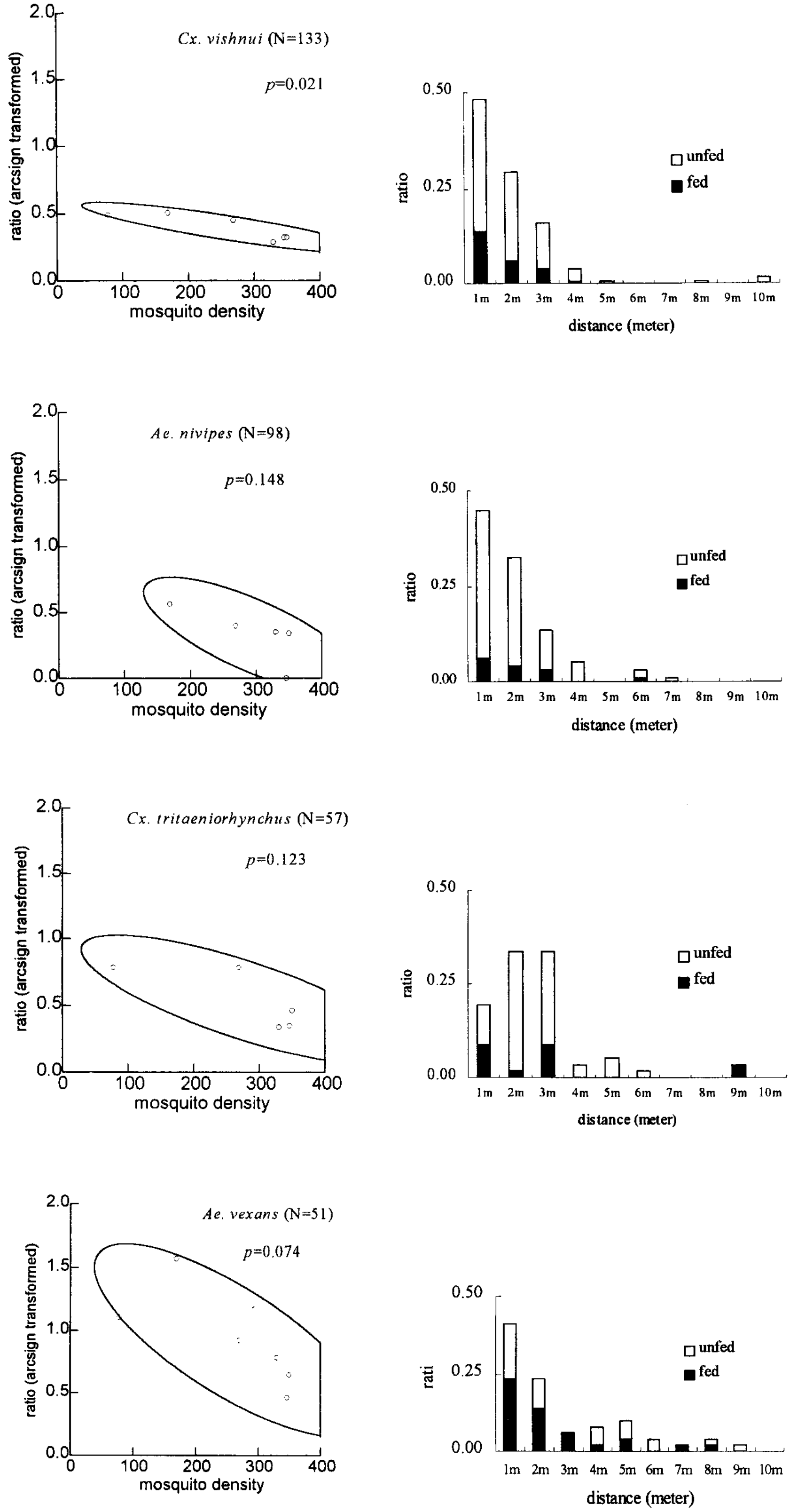

Fig. 2. Continued.

Table 4. Distribution of fed and unfed female mosquitoes from the bovine host at 1–10 m. Absolute numbers of fed and unfed females were changed into proportions against *N* (total number of fed and unfed females.)

			Distance (m) from host																			
			Fed females										Unfed females									
Species	No.	Fed ratio	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
Aedes lineatopennis	21	0.71	0.19	0.14	0.05	0.14	0.05	—	0.10	0.05	—	—	0.10	—	0.10	0.05	—	0.05	—	—	—	—
Ae. vexans	51	0.53	0.24	0.14	0.06	0.02	0.04	—	0.02	0.02	—	—	0.18	0.10	—	0.06	0.06	0.04	—	0.02	0.02	—
Anopheles aconitus	638	0.12	0.07	0.04	0.01	—	0.00	—	—	—	—	—	0.34	0.27	0.12	0.07	0.03	0.02	0.01	0.01	0.00	—
An. minimis	33	0.15	0.06	—	0.03	0.03	0.03	—	—	—	—	—	0.33	0.21	0.15	0.15	—	—	—	—	—	—
An. nivipes	98	0.14	0.06	0.04	0.03	—	—	0.01	—	—	—	—	0.39	0.29	0.10	0.05	—	0.02	0.01	—	—	—
An. peditaeniatus	173	0.53	0.16	0.14	0.10	0.05	0.03	—	0.01	0.01	0.01	0.01	0.18	0.13	0.07	0.02	0.02	0.02	0.01	0.01	0.01	0.01
Armigeres subalbatus	38	0.89	0.32	0.24	0.11	0.08	0.11	—	0.03	—	0.03	—	0.08	0.03	—	—	—	—	—	—	—	—
Culex gelidus	37	0.57	0.27	0.14	0.08	—	0.05	0.03	—	—	—	—	0.19	0.16	0.08	—	—	—	—	—	—	—
Cx. pseudovishnui	152	0.22	0.14	0.03	0.01	0.02	0.01	—	—	—	0.01	—	0.43	0.15	0.12	0.03	0.05	—	—	0.01	—	—
Cx. tritaeniorhynchus	57	0.23	0.09	0.02	0.09	—	—	—	—	—	0.04	—	0.11	0.32	0.25	0.04	0.05	0.02	—	—	—	—
Cx. vishnui	133	0.24	0.14	0.06	0.04	0.01	—	—	—	—	—	—	0.35	0.23	0.12	0.03	0.01	—	—	0.01	—	0.20
Mansonia uniformis	26	0.31	0.12	0.04	0.08	0.04	—	0.04	—	—	—	—	0.35	0.15	0.12	0.04	—	—	—	—	—	0.40

Patterns of mosquito distribution around the host

Table 4 summarizes the ratio of fed to total females and the data on distance from the cow for the 12 species (2 *Aedes,* 4 *Anopheles,* 1 *Armigeres,* 1 *Mansonia,* and 4 *Culex* species) that were sufficiently numerous to cluster. Four clustering methods (weighted and unweighted average, complete, and Ward minimum variance) gave very similar results; the other 3 methods resulted in uninformative chains. A representative phenogram (constructed by using the Ward minimum variance method) showed 2 distinct groups (Fig. 3): 1 of 5 species (*Armigeres subalbatus* (Coquillett), *An. peditaeniatus, Ae. lineatopennis* (Ludlow), *Ae. vexans,* and *Culex gelidus* Theobald = rapid group) and a 2nd of 7 species (*An. aconitus, An. nivipes, An. minimus,* Theobald *Ma. uniformis, Cx. vishnui, Cx. pseudovishnui,* and *Cx. tritaeniorhynchus* = slow group). The cluster analysis suggested that females of some species waited longer before feeding (we termed this group the slow group), whereas other species had a shorter preattack rest (the rapid group). The relationship between distance from the tethered cow and the proportion of fed or unfed females to the total number of females is shown in Fig. 4 (unfed females in the upper figure, fed females below). The proportion of the rapid group that had fed was higher than that of the slow group at every distance (t-test, Bonferroni adjusted $P = 0.003$, 0.001, and 0.006, at distances of 1, 2–4, and 5–10 m, respectively; Fig. 4). The proportion of unfed females was higher in the slow group than in the rapid group at 1 and 2–4 m (Bonferroni adjusted $P = 0.038$ and 0.007, respectively), but the proportions did not differ at 5–10 m. The rapid group also had higher overall proportions fed (t-test, pooled variance $t = 7.822$, df $= 10$, $P < 0.001$) than the slow group. Summarizing these differences, the species in the rapid group attacked the host more successfully than those in the slow group, so that unfed members of the slow group accumulated near the host (1–4 m).

DISCUSSION

Mosquitoes appeared to rest on the stakes primarily when a cow was present, and they were distributed randomly before approaching the cow (except *Ma. uniformis,* which approached from the east; perhaps its breeding site was close to the east of the study site). A comparatively high proportion of male *Ma. uniformis* was found on the stakes, whereas the samples of all other species were overwhelmingly female. Significantly more mosquitoes were collected from stakes closer to the host (1–4 m), for both fed and unfed females. The ratio of fed to total mosquitoes of the dominant species was negatively correlated with the total number of mosquitoes collected.

According to the definitions used in this paper,

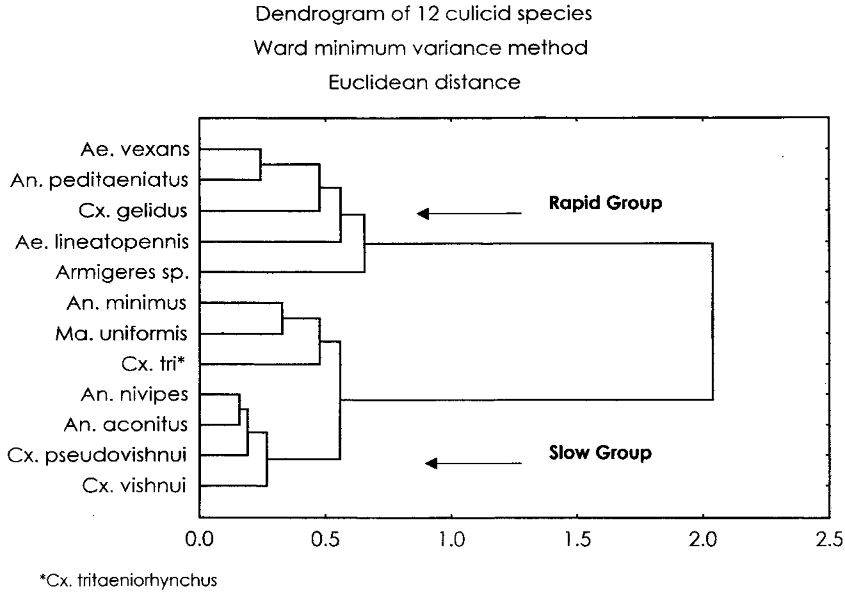

Fig. 3. Dendrogram for 12 culicine species resulting from cluster analysis (Ward minimum variance method with Euclidean distances) on the basis of Table 4. The rapid group had a shorter preattack rest than the slow group. Ae., *Aedes*; An., *Anopheles*; Cx., *Culex*; Ma., *Mansonia*.

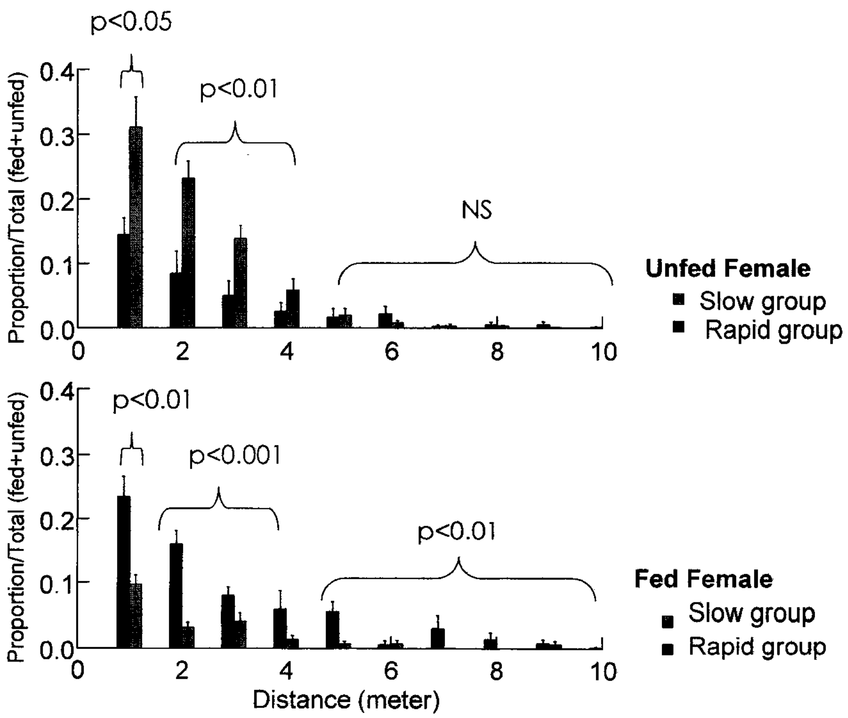

Fig. 4. Comparison of distributions of fed and unfed mosquitoes among rapid and slow groups. Absolute numbers of fed and unfed females were changed into proportional values out of the total females (fed + unfed) of each species. The upper figure shows the distribution of unfed females and the lower figure shows that of fed females. The vertical axis shows the mean value of the slow (longer preattack rest) and the rapid (shorter preattack rest) groups. The horizontal axis shows the distance from the host. Error bars show standard errors of the groups. *P*-values above vertical lines indicate significant or nonsignificant (NS) difference of the proportion in the distances (1 2–4, and 5–10 m from the host) between the groups (Bonferroni corrected *t*-test).

fed mosquitoes were those that presumably fed on the tethered cow. Fed mosquitoes might gradually distance themselves from the cow by slowly moving to the outer stakes. However, unfed mosquitoes may be unfed because of their recent arrival or because they are waiting to feed or have been unsuccessful at feeding; the experiment was not designed to distinguish these possibilities. We attribute the interspecific differences in the distribution of unfed mosquitoes to a lack of success in feeding by unfed females. Two observations support this inference. First, we noted different patterns of unfed mosquitoes between the 2 groups (slow and rapid). The unfed individuals in the slow group were closer to the cow than the unfed individuals of the rapid group. On the other hand, correlation of fed mosquito numbers in the rapid group with distance simply reflected the higher proportion that had fed. The other reason is that a negative correlation was found between the proportion that had fed and the total number of resting mosquitoes. This supports the postulate that mosquitoes remained near the cow because of a lack of feeding success. Viewed in this light, it is reasonable to conclude that the interspecific variation in the distribution of unfed females was due primarily to a lack of feeding success. Collections were made only until 11:20 p.m., and the unfed mosquitoes very likely fed on the host later in the night. This possibility does not deny our claim, because we analyzed the comparative spatial distribution of fed and unfed mosquitoes but not their abundance in number, which might increase later.

Wada (1969) quantified the nocturnal biting activity of *Anopheles sinensis* Wiedemann and *Cx. tritaeniorhynchus* by various methods (counts of mosquitoes alighting on pigs, on plates, or on tape set near a dry-ice bait) and found that the peaks of mosquito abundance differed among the methods. The number of mosquitoes counted at dry-ice–baited tapes showed 1 or 2 peaks, whereas counts of mosquitoes alighting on pigs were almost constant. He attributed this difference to the preattacking rest. The dry-ice–bait counts reflected the flight-activity rhythm of mosquitoes, which differed from the counts of mosquitoes attacking the pigs. We also observed a negative correlation between the number of resting mosquitoes and the proportion of fed mosquitoes. Consequently, numbers of fed mosquitoes were relatively constant, despite daily fluctuations in the number of mosquitoes captured (Table 2). What resources can be a factor limiting mosquito density on hosts? Host size makes blood an essentially unlimited resource. Possible limiting factors are available host skin surface area (Clements 1999) and host defense triggered by excessive attack. For example, a negative correlation between mosquito density and their feeding success due to the density-dependent defensive behavior of hosts has been reported (Edman et al. 1972, Waage 1979, Waage and Davies 1986). In cases in which large numbers of mosquitoes are present, prebiting resting can be adaptive to avoid host defensive behavior triggered by attacking. If this negative relationship between mosquito density and mosquito feeding success is a general rule (Kelly 2001), why is prebiting resting behavior only observed in some mosquito species? Our results showed that the density-dependent ratio of fed to total numbers differed among species (Fig. 2). Waage and Davies (1986) reported that intra- and interspecific competition occurred for tabanid species, which was associated with parasite density and host defensive behavior. At higher overall rates of fly landing, the alighting times on hosts of individual flies decreased as a result of increased host grooming. Prior experience with these density-dependent selective pressures might be a cause of observed preprandial differences of mosquito spatial distribution.

In conclusion, a prebiting rest was observed in several taxa of mosquitoes. We postulate that the prebiting resting is a period that allows the mosquito to evaluate many aspects of its host and decide whether to attack. Gillies (1980) showed that carbon dioxide generally attracts host-seeking mosquitoes. Most mosquitoes are attracted by general host cues, such as carbon dioxide and heat, whereas these general cues do not trigger biting in some species. Because they wait for their host in locations where general cues would be strongest, they might need other cues from the host to initiate successful feeding.

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